Amphibian Diversity, Distribution, and Habitat Use in the Yellowstone Lake Basin

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Abstract

Global amphibian population declines are being investigated through four interdependent fields of study: distribution and status, ecology, causes of declines, and environmental contexts. In Yellowstone National Park, work on amphibians has proceeded in all four of these fields. This paper describes amphibian species occurrence, distribution, and habitat-use patterns in the Yellowstone Lake area; summarizes the findings of a field study on habitat use by spotted frogs; and describes the directions and goals of continued amphibian investigations. Tiger salamanders, western toads, boreal chorus frogs, and Columbia spotted frogs all occur in the subwatersheds surrounding Yellowstone Lake. Chorus frogs and spotted frogs are the most common species. Salamanders are uncommon. Toads are rare, and we are concerned about their status in Yellowstone and in the Greater Yellowstone Ecosystem. A large variety of wetlands in the Yellowstone Lake basin provide breeding sites. Foraging and overwintering sites are also crucial to amphibian persistence. A case study of spotted frogs in the Lake Lodge area exemplifies this and underscores the need to understand habitat requirements, movement capabilities, and the effects of human activities. Amphibian investigations in Yellowstone over the next several years will probably focus on completing distribution surveys for inventory and monitoring purposes, research into habitat use and amphibian movements, and habitat mapping and modeling. The practical goal is an integrated information system that Yellowstone National Park can use for environmental analysis, project planning, monitoring, research, evaluation of ecosystem health, and education.

Introduction

At the end of the 1980s, biologists began discussing the possibility that many amphibian populations were rapidly declining and disappearing worldwide. By the end of the 1990s, there was general consensus that alarming declines had in fact occurred (Alford and Richards 1999). Within the context of the global reduction of wildlife and biological diversity, amphibian declines stood out for several reasons: the evolutionary durability of amphibians (survivors of at least three mass extinction events), the ubiquity of amphibians in terms of geography and habitat, the rapidity of the reported declines, and the occurrence of declines in protected and relatively pristine areas (Mattoon 2001).

During the last decade, there has been a large effort to understand the phenomenon of amphibian declines. Four main fields of investigation support and draw on each other:

1. Investigation of amphibian distribution and status is necessary to understand where species occur and to determine if declines have taken place or are in progress. Investigators compile historical and recent records for comparisons, and engage in extensive surveys and monitoring.
2. Natural history and ecology studies of populations in the wild teach us about population dynamics and habitat use, and help explain why populations are vulnerable to certain human-caused changes in the environment.
3. Investigation of the causes of declines is taking place in the field and in the lab. Multiple causes of declines have been identified, including habitat loss and modification, air and water pollution, damaging ultraviolet-B radiation exposure due to stratospheric ozone depletion, climate change, disease, introduction of non-native species, and complex interactions among factors.
4. Analysis of the environmental context using recent advances in geographic information systems (GIS), landscape component analysis, and other technologies allow investigators to map and model habitat and environmental change.

The ultimate goal of these investigations is to conserve and restore amphibian populations, which are important components of natural ecosystems. Investigators seek to provide information to land managers and to society that will stimulate and guide actions needed to maintain amphibian biodiversity and abundance.

In Yellowstone National Park, work has proceeded in all four of these fields of investigation. The effort to understand current amphibian species distributions in Yellowstone began at Idaho State University in 1988. By the mid-1990s, researchers from the Herpetology Laboratory at Idaho State University compiled historical, museum, and recent observation records and published a field guide (Koch and Peterson 1995). We have continued compiling observation and survey records in a Greater Yellowstone Ecosystem amphibian database (Van Kirk et al. 2000). Studies of distribution and occurrence have proceeded through a variety of survey projects, including surveys of roadsides and other areas targeted for development (e.g., Peterson et al. 1995; Patla and Peterson 1997; Patla 1997a), the northern range (Hill and Moore 1994), backcountry wetlands (e.g., Corkran 1997, 1998), and native fish restoration study areas (Patla 1998, 2000). Annual monitoring continues at six sites in the park (Peterson et al. 1992). In 2000, we began park-wide surveys through a joint effort with the U.S. Geological Survey (USGS) and its national Amphibian Research and Monitoring Initiative (Corn 2000) and the Vertebrate Inventory and Monitoring Project of the National Park Service (NPS). Investigators have engaged in studies of the causes of declines (Hawk and Peterson 1999; Hawk 2000) and field ecology studies of local populations (Hill 1995a, 1995b; Patla 1997; Patla and Peterson 1999). Finally, researchers from various institutions are designing habitat mapping and modeling projects. While the state of knowledge about amphibians in the park has advanced considerably over the past decade, we look forward to achieving a more precise understanding in the future about status, trends, ecology, and conservation of amphibians.

With respect to amphibians of the Yellowstone Lake area, this paper will describe what is currently known about species occurrence, distribution, and general habitat-use patterns. We will summarize the findings of a field study in the Lake Lodge area illustrating amphibian vulnerability to human-caused habitat changes. Finally, we will describe current and future directions and goals of amphibian investigations in Yellowstone.

Amphibian Occurrence and Distribution

To assess amphibian occurrence around Yellowstone Lake, we employed subwatershed units known as 7th-level Hydrological Units (HUs). Boundaries of these units were defined by a GIS coverage prepared by Yellowstone's GIS department. There are 48 subwatershed units around the lake. When we plotted locations of all known historical and recent records, we found that 27 units, or 56%, are known to have hosted, or currently host, amphibians (Figure 1).

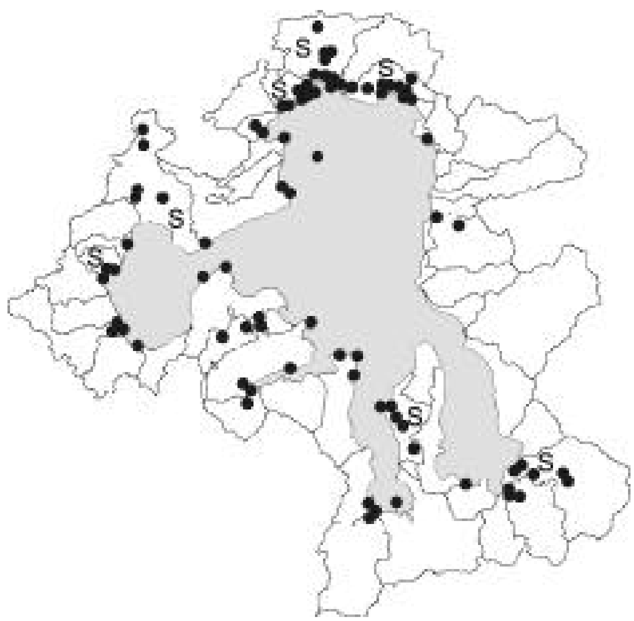

Figure 1. Yellowstone Lake with its 48 surrounding subwatershed units; dots show locations of historical and recent amphibian observations. Twenty-seven of the 48 units (56%) have amphibian records. The letter "S" indicates subwatershed units where formal amphibian surveys have been conducted in at least a portion of the unit within the past 10 years.

Formal amphibian surveys, following accepted protocols for detecting amphibian presence, have been conducted in only eight of the subwatershed units (Figure 1). One subwatershed (Arnica Creek) has been surveyed to identify amphibian breeding sites. Small portions of several other subwatershed units were surveyed during road improvement project analyses for the Arnica-to-West Thumb and Fishing Bridge-to-Canyon road sections. Portions of two subwatersheds, in the Promontory and Thorofare areas, were surveyed by volunteers in the late 1990s.

Knowledge about amphibian distribution in the Yellowstone Lake basin relies largely on incidental sighting reports. Incidental observations were provided by aquatic resources personnel doing fishery work, park rangers and other employees, exploratory surveys and observations by Idaho State University Herpetology Lab personnel, and other visitors. We regard distribution information for amphibians around Yellowstone Lake as incomplete, particularly for the east side of the lake and for roadless, remote areas.

The Yellowstone Lake area has a full complement of amphibian species: all those that one would expect to be present, based on their geographic range and occurrence elsewhere in the park, have been observed. While only four species occur, they are biologically diverse, representing two orders and four different families of amphibians. The tiger salamander *(Ambystoma tigrinum)* is from the order Urodela, the family of mole salamanders. In the order Anura, there is the western toad *(Bufo boreas)* from the family of true toads, the boreal chorus frog *(Pseudacris maculata)* of the tree frog family, and the Columbia spotted frog *(Rana luteiventris)* from the family of true frogs.

To judge from available data, the tiger salamander is surprisingly uncommon in the Yellowstone Lake area (Figure 2) given the abundance of this species in some other portions of Yellowstone, e.g., the northern range (Hill and Moore 1994) and Hayden Valley (Patla 2001). Some of this apparent rarity may be due to the fact that adult salamanders spend much of their time underground and are infrequently encountered by people except during periods of mass migration. Our Yellowstone Lake area dataset's reliance on incidental observation is thus likely to be biased against this species. However, the lack of observations of salamanders on the well-traveled roads north and west of Yellowstone Lake suggests that this species is in fact uncommon, or that salamander populations are much smaller than those of Yellowstone's northern range.

The western toad appears to be rare (Figure 3). We know of only two current breeding sites in the vicinity of Yellowstone Lake. There is much concern about this species because of dramatic declines elsewhere; in Colorado and southern Wyoming the western (boreal) toad *(Bufo boreas boreas)* is a candidate for listing under the Endangered Species Act. Toads and their tadpoles are conspicuous in comparison with salamanders. Adult toads disperse widely from breeding sites and may be seen basking in open areas on sunny days or crossing roads at night. Toad tadpoles and newly metamorphosed toadlets form large conspicuous congregations.

The boreal chorus frog is widespread (Figure 4), and probably common around Yellowstone Lake if the complete picture were known. Although adults are tiny and visually inconspicuous, the males call loudly in May and June, making this an easy species to detect at that time. Wetlands on the north side of Yellowstone Lake ring with the chorus of these frogs on spring evenings. Large

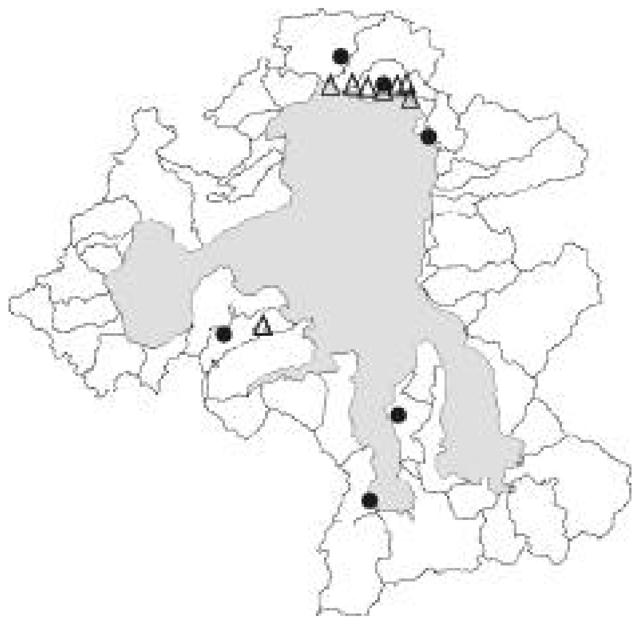

Figure 2. Locations of tiger salamanders, with triangles representing records prior to 1986, and dots indicating more recent records. Salamanders have been observed in a total of 7 subwatershed units (3 prior to 1986; 6 since 1986).

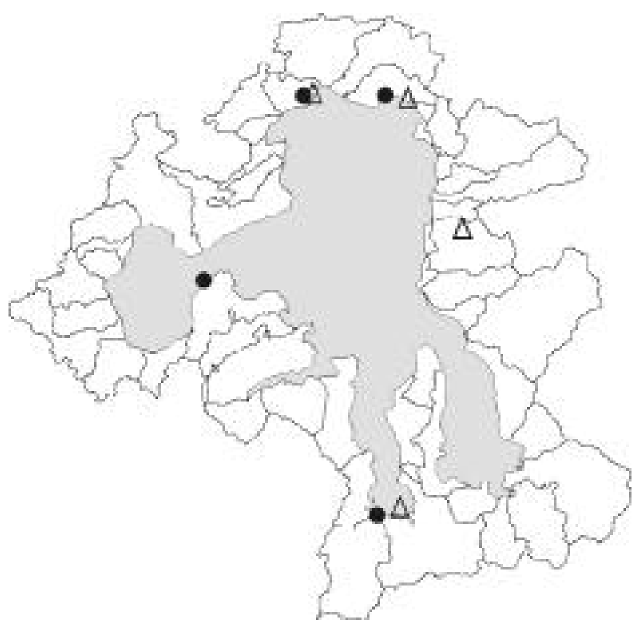

Figure 3. Locations of western toads, with triangles representing records prior to 1986, and dots indicating more recent records. This species has been observed in a total of 6 units (4 prior to 1986; 4 units since 1986).

numbers of metamorphs have been observed in lakeside wetlands on the south shore of Yellowstone Lake (Koch and Peterson 1995).

The Columbia spotted frog is also widespread (Figure 5). It is the most frequently seen amphibian in the Yellowstone Lake area and across much of the Greater Yellowstone Ecosystem. This is a visually conspicuous species: spotted frogs often bask on the edges of ponds and streams, producing a loud splash as

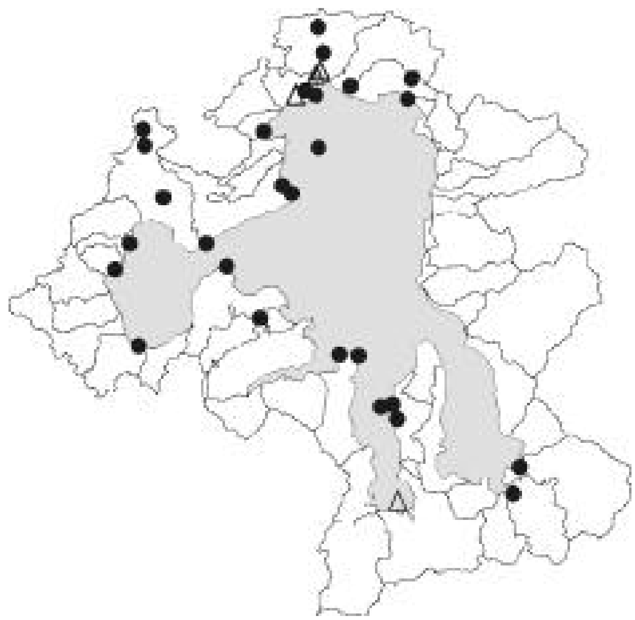

Figure 4. Locations of boreal chorus frogs, with triangles representing records prior to 1986, and dots indicating more recent records. This species has been observed in a total of 17 units (3 prior to 1986; 17 since 1986).

they hop into the water. Tadpoles of spotted frogs grow to a larger size than the other anuran species and are often easily visible in shallow water. Newly metamorphosed spotted frogs may be abundant as they emerge from breeding pools, although they tend to be more dispersed than toadlets.

In summary, based on the number of subwatershed units in which they have been observed, salamanders and toads are relatively rare around Yellowstone Lake, while chorus and spotted frogs are more common and widespread (Figure 6). Historical or pre-1986 information is so scant for most of the area that it does not reveal much about possible trends. For most amphibian species in Yellowstone, the more effort that is expended in searching for them and keeping track of observations, the more locations are recorded. However, this is only marginally true for toads, as is indicated by the relatively small difference between historical and recent records shown in Figure 6. We think it is likely that western toads have declined in the Greater Yellowstone Ecosystem, based on the records

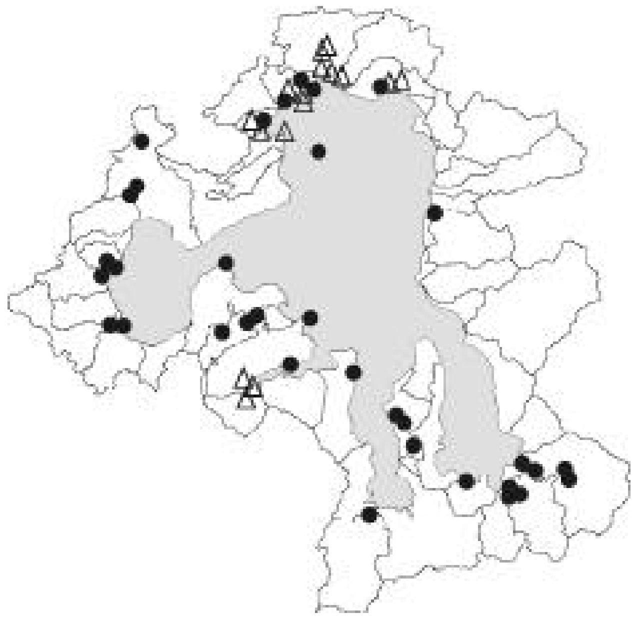

Figure 5. Locations of Columbia spotted frogs, with triangles representing records prior to 1986, and dots indicating more recent records. This species has been observed in a total of 22 units (8 prior to 1986; 18 since 1986).

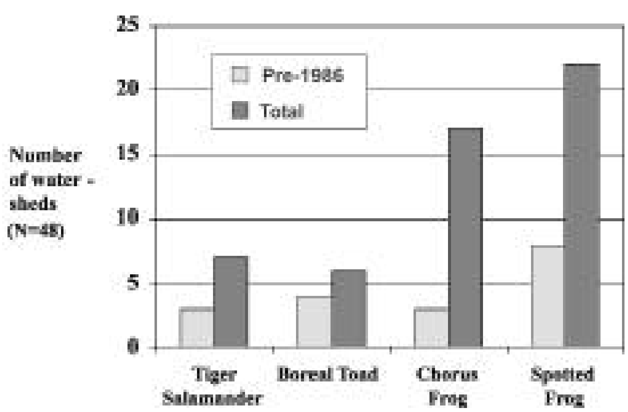

Figure 6. Number of subwatershed units around Yellowstone Lake where amphibian species were observed prior to 1986, and total number of watersheds (including all records, historical and recent) where species were observed.

and notes of earlier researchers and their current scarcity (Koch and Peterson 1995; Van Kirk et al. 2000).

Habitat Use

All amphibian species of Yellowstone rely on ponded or very-low-gradient water for reproduction. Eggs and larvae are aquatic obligates and will perish if breeding sites dry up before development is complete. The Yellowstone Lake area offers a variety of breeding sites for amphibians. Western toads in the Greater Yellowstone Ecosystem breed predominantly in water with high conductivity, often geothermally influenced (Hawk and Peterson 1999; Hawk 2000). These generalizations hold true for the two known toad breeding sites around Yellowstone Lake; toads breed on the west side of Indian Pond where conductivity often ranges above 1,000 FS (Patla and Peterson, unpublished data) and in a thermal pool at Breeze Point (reported by fisheries crew, 1999). The other amphibian species breed in a variety of temporary and permanent ponds in forests and meadows, generally with emergent vegetation. Acidic waters (< pH 6.0) are apparently not used as breeding sites (Patla and Peterson 1997), although this hypothesis needs more investigation. Lagoons and shallow-water marshes at the mouths of creeks draining into Yellowstone Lake, e.g., the mouths of Lodge and Pelican creeks, are known to provide breeding sites that produce large numbers of chorus frogs and spotted frogs.

Finding and documenting breeding sites is the focus of amphibian surveys. Amphibians have a very strong fidelity to breeding sites: some that were known to be used 50 years ago in the Yellowstone Lake area are still active. To monitor amphibians across the Greater Yellowstone Ecosystem and determine if statistically significant declines are occurring, investigators plan to track changes in the number of active breeding sites per species over time.

Breeding sites, however, are obviously only part of the habitat picture. It is quite common to find ponds inhabited by thousands of tadpoles, but with few or no adults in sight following the brief season of mating and egg deposition. The reason for this is very significant in the ecology of amphibians of the temperate zone. In many cases, habitat units that are necessary for amphibians to carry out their lives are spatially separated. Amphibians leave the breeding site to go to prey-rich areas for summer range, and then move on to places where they can safely winter. Biologists are just beginning to get an appreciation for how far amphibians can and do migrate to access breeding, foraging, and over-wintering sites (Pilliod 2001). Maximum migration distances range from 3 to 15 km for some populations (Sinsch 1990). Understanding of amphibian distribution will advance as researchers gain more knowledge about the spatial relationships of habitat components, natural history and habitat requirements that are unique to each species, and habitat-use and movement patterns in a variety of environmental settings.

Case Study at Lodge Creek

Habitat-use patterns of a spotted frog population in the Lake Lodge area have been the subject of historical and recent field studies. In the 1950s, Frederick Turner, a graduate student at the University of California–Berkeley, studied population dynamics and spatial relationships of the spotted frogs inhabiting a 28-ha area around the headwaters of Lodge Creek, between Fishing Bridge and Lake Village (Turner 1960). In the 1990s we repeated Turner's mark–recapture study of the population to compile comparable datasets. We found that the population had sharply declined and that habitat-use patterns had changed (Patla 1997b; Patla and Peterson 1999). Between the two study periods, the frogs' habitat was altered by several development projects, including reconstruction and relocation of the Grand Loop Road in the 1970s, increased residential development, horse-pasture use and maintenance, and increased development and use of Lodge Creek springs for the water needs of Lake Village. In addition to direct habitat losses, habitat fragmentation occurred. A migration corridor linking breeding and over-wintering habitat was interrupted by the path of the new section of the Grand Loop road. Breeding in the affected pool dwindled and finally ceased completely by 1995, and frog numbers in that portion of the study area have declined most severely (Patla 1997b; Patla and Peterson 1999).

This case study exemplifies how important it is for amphibians to have access to all habitat components. It also underscores the need to understand what habitats each species relies on to complete its life cycle, what constitutes constraints to amphibian movements, and how human activities and development projects may adversely affect amphibian populations. In the case of spotted frogs, it is likely that their dependence on non-freezing water (springs or spring-fed water bodies) for winter habitat limits their distribution and persistence in local areas as strongly as the availability of breeding sites (Pilliod 2001; Pilliod and Peterson 2001). Wintering and foraging habitat requirements, and their variability in different environmental contexts (e.g., at different elevations and in different plant communities), are as yet poorly known for Yellowstone amphibians.

Amphibian Studies in Yellowstone

As an overview of current and future amphibian studies in Yellowstone, we envision continued work in three main areas (Figure 7).

Distribution and status. We are conducting amphibian surveys in randomly selected 7th-level hydrological units (HUs) in Yellowstone and Grand Teton national parks. To achieve geographical distribution across Yellowstone, we selected HUs for survey from every third square in a grid placed over the park. As of the end of the 2001 field season, the surveys in Yellowstone are about 30% complete: 11 of the 36 targeted units have been surveyed. Supported by the USGS's Amphibian Research and Monitoring Initiative and NPS's Greater Yellowstone Area Inventory and Monitoring Program, this project will describe the distribution and abundance of breeding populations and considerably extend our current knowledge. The surveys are designed to serve as the basis for monitoring trends and answering questions about potential declines. Depending on funding levels, surveys of the selected units should be completed within three years. The project also includes targeted surveys for species of special concern in Yellowstone and more intensive population monitoring at selected sites.

Environmental context. One of the primary objectives of our amphibian studies is to develop GIS models and maps to indicate the probability of habitat

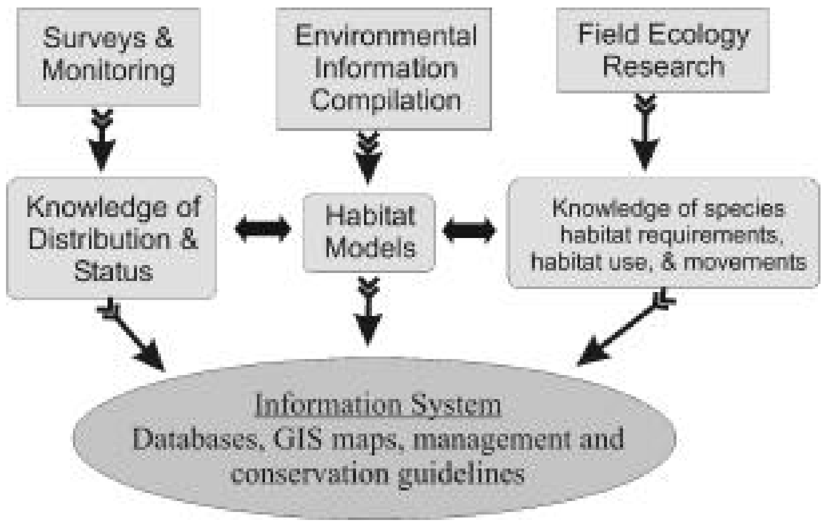

Figure 7. Overview of amphibian investigations. The information system resulting from integrated efforts will have multiple purposes, including amphibian conservation, resource management and protection, interdisciplinary research, and education.

use by amphibians at different times during their life cycle (e.g., breeding, foraging, dispersing, and overwintering). This requires information about environmental conditions (e.g., topography, temperatures, cover types, water quality, and the presence of other species) as well as information about amphibian natural histories (see below). The lack of high-resolution spatial and spectral data is probably the single most important factor limiting the use of GIS to design, analyze, and apply the results of amphibian surveys (Peterson et al., in press). Researchers from Idaho State University, Montana State University, the USGS National Mapping Division, and the Yellowstone Ecological Research Center are taking several approaches to address this issue, including: (1) using high-resolution hyperspectral imagery to identify small wetlands suitable for amphibians; (2) developing GIS and statistical models to predict wetland habitat (based on a variety of information sources, such as digital elevation models, hydrology, and remote sensing), and (3) combining the habitat data with amphibian-use information to develop statistical and GIS amphibian habitat models. These projects seek to integrate advances in landscape analysis with knowledge garnered from amphibian surveys and ecological field studies. With tools provided by these projects, we will be better able to identify and map amphibian habitat, predict amphibian occurrence, and assess potential effects of environmental change and proposed management activities.

Natural history and ecology. Researchers from Idaho State University and other facilities will carry out ecological field studies to elucidate habitat associations and requirements, habitat use, and amphibian movements. Investigations will include population-level studies using mark–recapture techniques, and focal animal studies employing radio-tracking and behavior observation. This labor-intensive field research is vital for the creation and verification of habitat models. Studies are also needed to determine how local populations are connected to each other through dispersal or immigration of individuals, and how important these connections might be for population persistence.

Information integration. These three fields of effort are interactive. Data from amphibian surveys will be used for habitat mapping and modeling, and the models will predict amphibian distribution and occurrence park-wide. Findings of amphibian ecology and movement studies will also contribute to mapping and modeling, which in turn can be used to develop and test hypotheses about habitat associations, ecological relationships, and the causes and patterns of population declines. The products of these investigations will be integrated to form an information system for the park and other agencies interested in amphibian declines and conservation (Figure 7). Uses of this information system could include environmental analysis, project planning and engineering, amphibian conservation at local and regional levels, monitoring, evaluation of ecosystem health and changes, interdisciplinary research, and public education.

Acknowledgments

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Sublacustrine Geothermal Activity in Yellowstone Lake: Studies Past and Present

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Abstract

The discovery and description of hydrothermal features such as geothermal vents, gas fumaroles, and even geysers within Yellowstone Lake is presented. Research was carried out over a period of 17 years beginning in 1984 and employed SCUBA to observe the sublacustrine hot springs and microbial mats in Sedge Bay, Yellowstone Lake. These initial observations led to the use of a remotely operated vehicle (ROV) to observe, sample, and study hot springs and gas fumaroles in the deepest regions of the lake, off Stevenson Island, in waters over 120 m deep. Relict hydrothermal structures varying in size (from centimeters to meters in height) and shape (from solitary pipes or chimneys to irregularly shaped structures) were located and sampled in various areas of the lake, including Mary Bay, Bridge Bay, and West Thumb.

Introduction

Yellowstone Lake, at an altitude of 2,356 m and with a surface area of ~342 km^2, is the largest high-altitude lake in North America. The lake is a natural habitat for the cutthroat trout *(Oncorhynchus clarki bouvieri)* and provides an important sports fishery for tourists that pass through Yellowstone National Park each summer (Gresswell et al. 1994). The fishery, combined with the lake's pristine beauty, is enough to make it an important resource. However, because it is located in Yellowstone National Park, one of the most tectonically and geothermally active regions of the world, it has an additional characteristic that makes it even more interesting: hydrothermal vents.

The Yellowstone plateau, with an average elevation of about 2,000 m, overlies magma chambers that are the source of the heat for the well-known geothermal features in the park: geysers, hot springs, fumaroles, and mud pots (Eaton et al. 1975). Like the Hawaiian Islands, Yellowstone lies over a hot spot in the earth's crust. Over the last 2.1 million years there have been three major volcanic episodes in the Yellowstone area; the most recent of these, the eruption of the Lava Creek Tuff of the Yellowstone caldera, occurred approximately 0.65 million years ago. During this last episode more that 900 km^3 of rhyolitic pumice and ash erupted, resulting in the collapse of a 75 x 45-km area and the formation of the Yellowstone caldera. Following this collapse, the rising magma chamber uplifted the floor of the caldera and formed two resurgent domes within the caldera boundary (Christiansen 1984; Good and Pierce 1996).

Most of the park's well-known geysers and hot springs occur within the Yellowstone caldera (Figure 1). Groundwater within the park percolates down through cracks and crevices in the rock and is heated to above boiling when it nears vast underground reservoirs of magma (Fournier 1989). It then resurfaces to create the park's famous thermal features, such as Old Faithful and Mammoth Hot Springs. What was generally unappreciated until the 1980s was that much of this same activity also occurs in Yellowstone Lake.

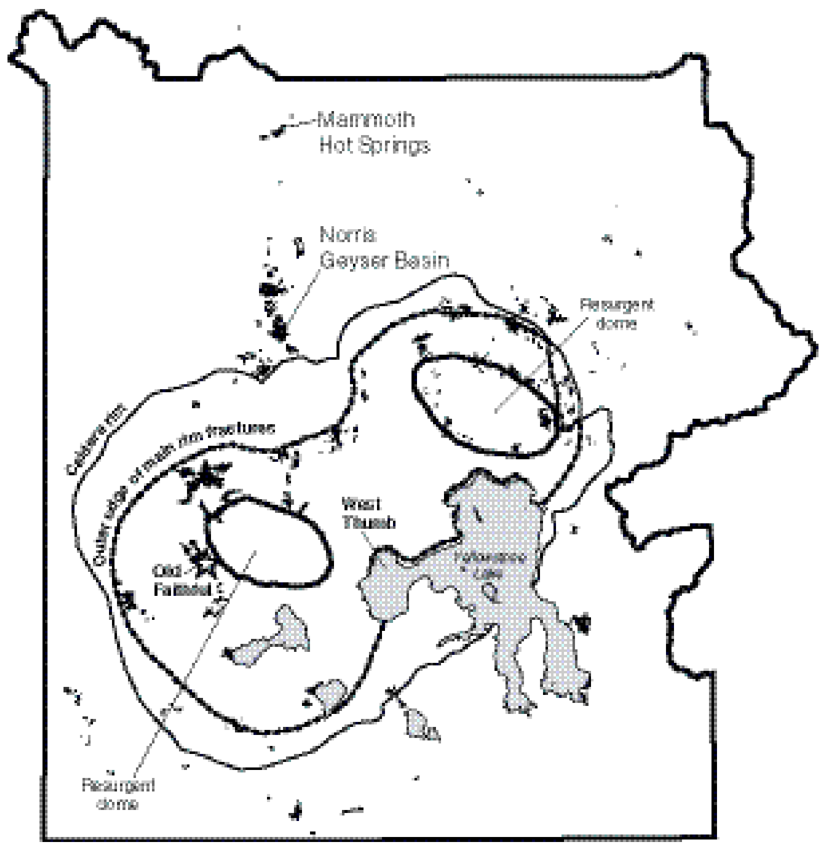

Figure 1. Line drawing of Yellowstone National Park showing Yellowstone Lake and various geothermal features nearby. Also shown is the boundary of the old caldera rim and its relationship to the lake. From Remsen et al. 1990.

In 1983, a small group of limnologists and other researchers from the University of Wisconsin–Milwaukee's Center for Great Lakes Studies visited Yellowstone National Park to collect some sediment cores from the West Thumb Basin and other areas of Yellowstone Lake. The objective of our work at that time was to examine these cores from a historical perspective and to see if we could re-create, or estimate, the productivity of the lake over the past several hundred years. The National Park Service (NPS) was interested in this study because other scientists (Shero and Parker 1976) previously hypothesized that Yellowstone Lake productivity had consistently decreased over the last 1,500 years and that this decrease might be related to long-term decreases in nutrient supplies. Declining nutrients available for the growth of algae—and, in turn, fish—had ominous overtones for the cutthroat fisheries in Yellowstone Lake. This appeared to contradict the norm, in that most lakes become more eutrophic over time and in some cases actually fill in, as in the case of bog lakes. Shero and Parker (1976) suggested that the decrease in total nutrient supply might be related to decreases in annual precipitation.

During this study in 1983, it was observed that some of the park's thermal basins literally rested on the shores of the lake, and, while working in the West Thumb Basin, bubbles were observed breaking the surface of the lake. These observations, combined with thermal gradient data from the lake floor (Morgan et al. 1977; Blackwell et al. 1986) indicated the presence of hydrothermal activity within the lake itself. Areas of geothermal activity were noted, and were examined in greater detail the following summer.

Thus began a study that continues until this day. At the time an initial research proposal was submitted to the National Geographic Society, very little was known about sublacustrine hydrothermal systems in Yellowstone Lake, or for that matter in other lakes around the world in which hydrothermal activity was known or suspected to occur. Presented here is a general review of the discoveries made while investigating the sublacustrine geothermal activity in Yellowstone Lake over the past seventeen years.

Research in Yellowstone Lake: Observations with SCUBA Divers

The first extensive search for underwater geothermal activity in Yellowstone Lake occurred from 1984 through 1986 in Mary Bay and in an adjacent bay to the south of Steamboat Point that we have called Sedge Bay (Remsen et al. 1990). Sedge Bay became an attractive site because there was a large emergent rock at the foot of a picnic area off the main road, where mobilization for our diving activities could occur. From the rock, approximately 12 ft from shore, diving excursions were made to the shallow-water vent areas (approximately 1 ha) and adjacent communities. SCUBA diver observations in these shallow bays (< 7 m deep) revealed a variety of geothermal features, including numerous fields of gas fumaroles, hot-water springs, and spectacular microbial mat communities (Remsen et al. 1990). Curtains of gas bubbles consisting mainly of carbon dioxide (plus, occasionally, some methane and hydrogen sulfide) and other nutrients were observed emanating from barren sandy sediments where temperatures reached 100°C at 5 cm below the surface (Klump et al. 1988). In these sandy areas, the gas fumaroles often formed a series of 10- to 12-cm domes created by the sorting of sandy sediments entrained in rising gas bubbles, resulting in the deposition of the finer-grained particles at the periphery of the gas vent. The hot gas vents were found dispersed over the barren sandy bottom as well as originating in areas of dense submergent plant growth. Gas fumaroles that contained hydrogen sulfide and also made contact with macrophytes *(Potamogeton, Ranunculus, Drepanocladus,* aquatic mosses, and filamentous algae) often produced conditions ideal for the colonization of chemolithotrophic bacteria: sulfide-oxidizing bacteria that actually use sulfur compounds as food from which they build new bacteria. When this occurred, white filaments could be seen attached to the plants (Figure 2). These particular bacteria (known as *Thiothrix* spp.) form long filaments that coil upon themselves. Similar bacteria have been found around hot vents in the ocean as well (Ruby and Jannasch 1982).

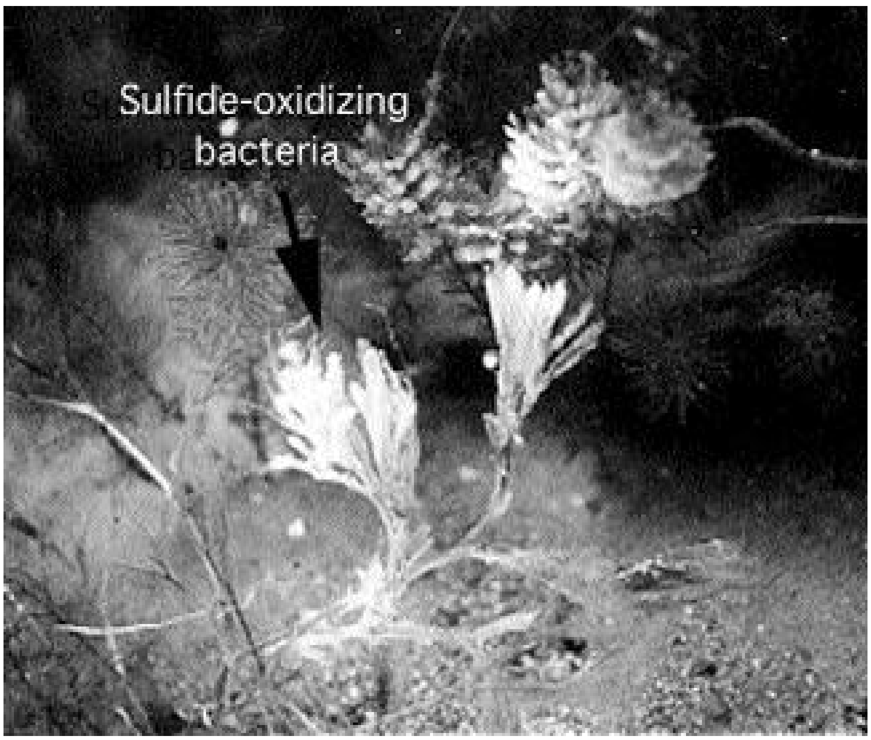

Figure 2. Photograph of macrophytes in Sedge Bay, Yellowstone Lake, coated with sulfide-oxidizing bacteria (arrow). Photo by J. Val Klump. ISWW/UWM Great Lakes WATER Institute.

Hydrothermal springs within the lake bottom create a range of thermal and chemical gradients that promote the growth of different types of bacteria as well as higher forms of microorganisms not typically found in deep, cold, nutrient-poor lakes. These gradients have resulted in the development of microbial mats (Figure 3) containing purple and green photosynthetic sulfur bacteria, sulfide-oxidizing bacteria, algae that can use the energy of the sun in the absence of oxygen (anoxyphotosynthetic cyanobacteria) as well as a wide variety of nematodes, protozoa, and other small animals that feed on these bacteria (Remsen et al.

1990). Enrichment culture techniques employed back in our university laboratories have yielded a diverse group of microorganisms, including methane-oxidizing bacteria, photosynthetic bacteria, thermophilic sulfate-reducing bacteria, and others. Similar types of microorganisms have been found attached to natural sur-

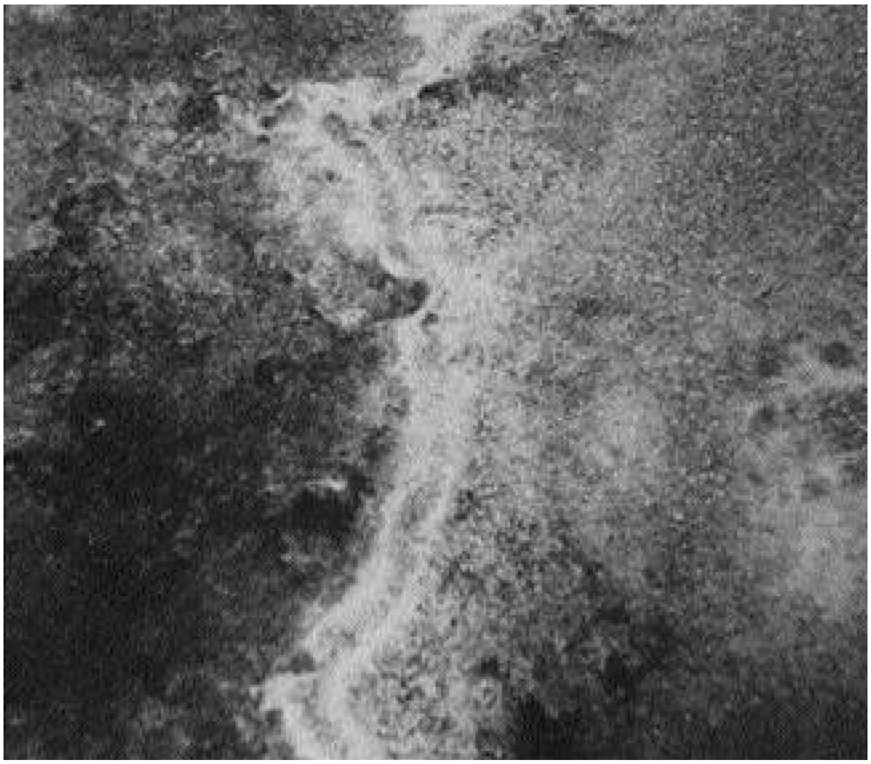

Figure 3. Photograph of a portion of a microbial mat located in Sedge Bay, Yellowstone Lake. The chemical and temperature gradients that exist in these mats determine the types of micro- and macro-organisms present in the mat. Photo by J. V. Klump, UWS/UWM Great Lakes WATER Institute.

faces near oceanic hydrothermal vents at the Galapagos spreading center in the Pacific Ocean, in the Quaymas Basin of the Sea of Cortez, and on sediments and rocks in Crater Lake, Oregon (Jannasch and Wirsen 1981; Tuttle et al. 1983; Dymond et al. 1989).

Dense populations of oligochaete worms were found congregated near many of the fumaroles on the down-current side. These fumarole colonies were circular, distinctly formed units compared with the sparsely colonized substrates away from fumaroles. Worm abundances were about an order of magnitude greater at the fumaroles than away from the vents. The fumarole worm colonies were made up of three tubificid oligochaete species, *Limnodrillus hoffmeisterii*, *L. udekemianus,* and *L. profundicola* (Brinkhurst and Jamieson 1971). The worms' normal orientation in the sediments is to have their front end (and mouth) pointed down in the sediment, while their back end is projected up and into the water. Usually their front end is as much as 1.5 inches deep in the sediment; however, it is unlikely that they are that deep when near hot-water vents, where the temperatures can reach nearly 80°C. The worms are most likely attracted to the vents in part because of the healthy bacterial flora supported by the nutrient and thermal activity of the fumaroles.

Generally speaking, when temperatures in sediments were less than 30°C, vegetative growth in the form of mosses and other macrophytes flourished; however, when temperatures increased and began to approach 40-50°C, then plant growth was absent. This phenomenon was quite evident in Sedge Bay, where ambient water temperatures approached 15°C at the time; the hypothesis for these observations was that the establishment of temperature and/or chemical gradients (radiating from the center of maximum vent activity) could provide

Table 1. Concentrations of ions and nutrients dissolved in hydrothermal vent waters and surface waters in Sedge Bay, Yellowstone Lake. Source: Klump et al. 1988.

Sample Vent	Cl^-	SO_4^{2-}	Mg^{2+}	Ca^{2+}	Na^+	K^+	SiO_2	NH_4^+	ΣCO_2
	(μM)								(mM)
4	97	113			425	73	27	19.9	
5	100	99	176	196	532	63	150	2.2	
6	99	592	2,900	2,300	4,100	535	2,429	17.9	28.9
8	102	734	2,700	2,300		510	2,429	23.2	26.6
9	113	442	1,900	1,600	3,200	401	2,429	93.1	10.1
10	68	566					1,829	33.7	19.2
11	94	634					2,429	22.7	25.9
12	179	187					341	27.3	5.25
13	95	556	2,400	2,000	3,800	519	3,172	36.8	
14	87	503			3,800	496	3,074	39.7	
15	79	532	2,300	1,900	3,700	501	3,152	53.8	19.4
16	193	348	2,900	2,400	4,700	606	3,290	23.1	25.6
17	211	349	2,700	2,200	4,400	528	3,310	74.3	24.1
19	659	173	1,700	1,000	4,600	536	3,113	80.4	16.0
20	950	98	395	290	3,600	420	2,033	218.0	6.34
22	179	366	2,800	2,200	4,400	554	3,211	0.0	25.5
23	156	286	2,000	1,600	3,200	413	2,387	41.6	14.5
Lake water (average of all samples)									
	149	80	102	143	490	46	167	0.15	0.66
±	24	6	2	3	27	3	8	0.25	0.06

hydroponic conditions conducive for plant growth. However, it is now known that the hydrothermally influenced waters are high in dissolved carbon dioxide, ammonium, silica, phosphate, and sulfide, and that fumarole gases are primarily carbon dioxide (Tables 1 and 2; Klump et al. 1988, Remsen et al. 1990).

A New Technology: The Remotely Operated Vehicle

Starting in 1987, a remotely operated vehicle (ROV) has been employed in the underwater studies of Yellowstone Lake. Over 280 separate dives by the ROV were made over the period 1987–1999 (Table 3). It has provided direct observations of even the deepest areas of the lake, off Stevenson Island, in over 120 m of water.

Table 2. Chemistry of hydrothermal fluids collected from sublacustrine hydrothermal springs in Yellowstone Lake, 1988–1989. Source: Remsen et al. 1990.

	Cl^-	$SO_4^=$	NH_4^+	K^+	Na	pH	ΣCO_2	NH_4^+	SiO_2
	(mM)	(µM)	(µM)	(µM)	(mM)		(mM)	(µM)	(µM)
Mary Bay: Storm Point Vent (n = 11)									
High	3.30	45	82	1,157	3.91	7.20	16.13	22.4	1.620
Low	2.50	32	57	947	3.23	6.85	14.03	6.8	861
Mary Bay: Pipe Garden Vent (n = 13)									
High	0.171	111	11.1	51	0.83	6.18	5.34	30.6	355
Low	0.164	96	2.0	44	0.69	5.28	2.02	7.1	197
Sedge Bay Vents (n = 17)									
High	0.95	734	93.1	606	4.7	nd	28.9	nd	3,310
Low	0.07	99	17.9	401	3.2	nd	5.3	nd	2,030
Average ambient lake water									
Mean	0.16	87	0.15	45	0.64	6.89	0.80	0.44	
Sdev	0.01	4	0.25	3	0.06	0.11	0.06	0.23	8

Table 3. Number and location of ROV dives, Yellowstone Lake, 1987–1999.

	'87	'88	'89	'90	'92	'94	'95	'96	'97	'98	'99	Tot
Sedge Bay	3	2	1	2		2			1	1	3	15
Mary Bay	7	6	18	11	7	21	19	7	7	13	6	122
Storm Pt			4	3	1							8
Steamboat Pt			1	1	2		6	1	2		1	17
Pelican Roost	1	1									7	9
Stevenson Is	5	7	7	7	1	6	1		1	7	2	44
Off Lake			1									1
Bridge Bay				1		4		6	2			13
West Thumb	2				5		6	1	13	14	7	48
Pumice Pt					3							3
Dot Is					1							1
Breeze Pt								1				1
Wolf Pt								1				1
Southeast Arm					1							1
Total	18	16	32	24	21	30	34	16	30	37	26	285

With hundreds of small "microquakes" shaking Yellowstone every year, possibly triggering underwater landslides and changes in hot-water flows, sending a manned submersible into the depths of Yellowstone Lake would be very expensive and extremely risky. Thus, our little yellow submarine (Figure 4), later modified into a larger "open-frame" ROV (Figure 5), became vital to unlocking the

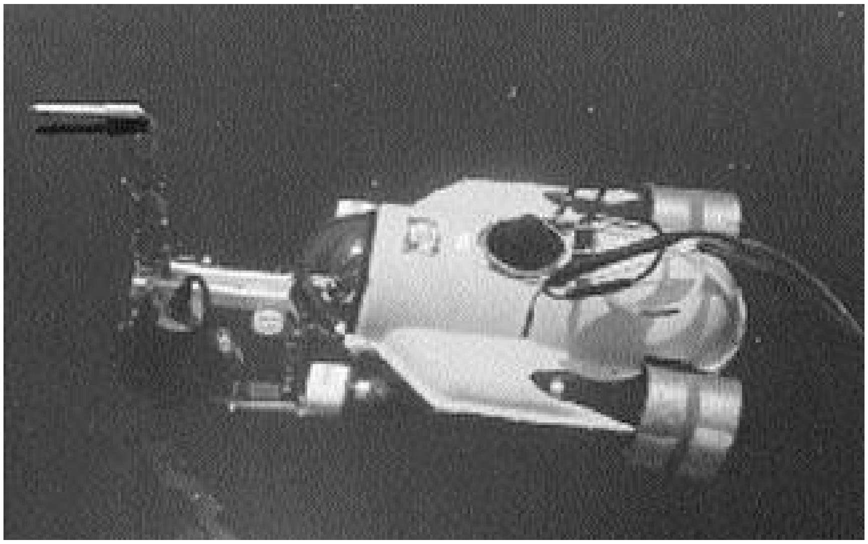

Figure 4. Photograph of early version (1987) of ROV used in these studies. Photo by C. C. Remsen, UWS/UWM Great Lakes WATER Institute.

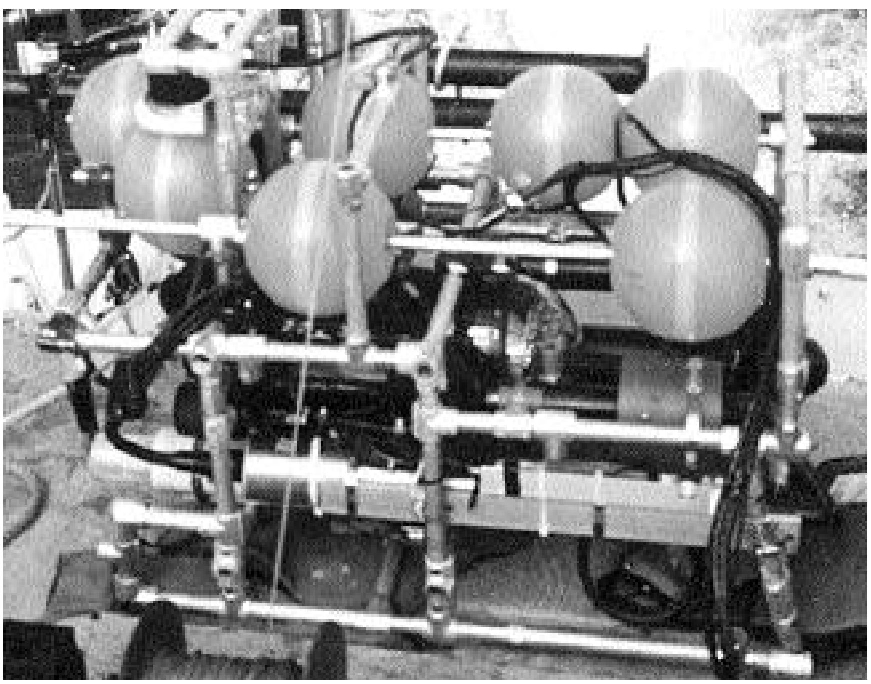

Figure 5. Photograph of a later version (1996) of ROV used in these studies. Note the use of an "open frame" which allows the attachment of various sensors, cameras, and water sampling devices. Photo by C. C. Remsen, UWS/UWM Great Lakes WATER Institute.

secrets of Yellowstone Lake, particularly in the deeper waters where SCUBA diving was not practical.

Early designs of the ROV, with a mass of ~18 kg, allowed us to take video footage and confirm the presence of hot springs and fumaroles at numerous locations and depths throughout the lake. However, the successors of the early yellow submarine, which have a mass of about 115 kg, have provided a more sophisticated and useful system (Klump et al. 1992). The growth and development of the ROV system was something that evolved over time and, like any evolutionary process, continues today.

Briefly, the main ROV pressure housing contains control electronics, a video camera, and a vertical thruster, with horizontal thrusters on either side of the housing. For navigation, combinations of sonar, fluxgate compass, and a magnetic compass are used, all housed separately on the open-frame ROV. At various times throughout its development and use, an array of sensors has been used on the ROV. Consistently, temperature sensors are used to monitor ambient and vent water temperatures (Figure 6). Conductivity sensors have also been used, and, as needed, a multi-probe (Hydrolab Model 4) has been attached to the ROV for extended sampling capabilities. Other instruments have included a three-function manipulator, a 16-loop water sampler (Lovalvo and Klump 1989), a Sipper system that uses a series of 60-ml syringes, and a motor-actuated pump from the surface to sample water. Prior to 1986, the largest water sample collected by the ROV was 10 ml. Subsequently, improvements in the system enabled us to collect 60-ml samples, and, finally, 1-l samples.

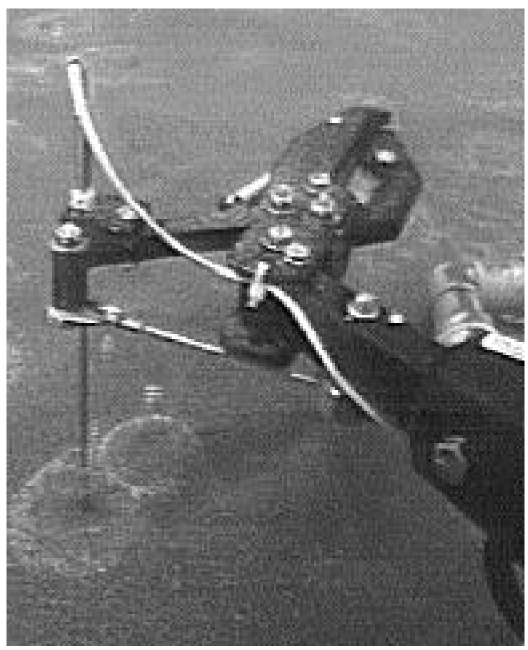

Figure 6. Photograph, grabbed from video, of ROV manipulator arm equipped with a temperature sensor, probing a small gas fumarole in Mary Bay, Yellowstone Lake. Note white "ring" around the fumarole; this is precipitated sulfur that has been produced by the oxidation of sulfide present in the fumarole gas. Video by David Lovalvo, Eastern Oceanics, Inc.

The manipulator is used for grasping objects or positioning equipment directly in a vent stream, or handling a scoop for collecting and storing larger objects, or as a "slurp gun" for collecting sediment samples. Having described all of this, anyone familiar with ROV technology and field research will know immediately that many, many hours in the field have been spent modifying equipment that failed or malfunctioned, or had to be improved or adapted on the spot. In this type of work, science definitely drives the technology, and many hours were spent late into the cool summer nights repairing and modifying equipment so that it would be ready at daybreak the following day.

The Underwater World of Yellowstone Lake: General Observations

In 1989, 30 dives over 12 days of "on the lake" work were completed. Seven stations in the eastern portion of the lake were occupied; however, the main focus of the study was on three stations in Mary Bay, the area of the lake with the highest heat fluxes (Wold et al. 1977) and highest excess radon concentrations (Klump et al. 1988), both indicators of considerable geothermal activity. In addition, a great deal of time was spent at a station in the central basin of the lake, off Stevenson Island, in an area with the deepest sounding of the lake, discovered just two years earlier in 1987 (Remsen et al. 1990; see also Kaplinski 1991). All of these locations were indicated to have sublacustrine geothermal activity, based upon the heat gradient data of Morgan et al. (1977; personal communications).

The Mary Bay sites, especially in a "deep hole" area (~50 m deep), have provided the greatest wealth of samples, including hydrothermal vent fluids (Table 2), fumarole gases, and samples of deep-living benthic communities. The most spectacular of these were the sponge communities colonizing rock and hard clay outcrops, microbial mat material, geological samples of fossil hydrothermal vent chimney or pipes, and other concretions. Within this "deep hole" or depression, the lake bottom is characterized by overhanging slopes of exposed lake sediments, slumps, hummock-like features, and amorphous concretions at scales ranging from 0.1 to 10 m (Klump et al. 1992).

First seen in 1987–1988, and then again in 1989 and in abundance in 1990 (as well as in the subsequent expedition years), were relatively flat sponges (Figure 7), each approximately 2–5 cm in diameter, found at a depth of 45–55 m in a region of high geothermal activity in Mary Bay. These sponges are usually identified by the silica "spicules" that are common to all sponges but are like fingerprints in that no two are alike. Henry M. Reiswig and Anthony Ricciatilis from the McGill University have identified sponges collected in Mary Bay from spicules and fragments as *Ephydatia fluviatilis* (Linnaeus, 1758). A specimen has been deposited in the Redpath Museum Invertebrate Collection as number 94-1-23.1. As mentioned, these sponges are usually (but not exclusively) found in the deeper waters of Mary Bay where the ambient temperature, warmed by geothermal heating deep within the sediments, remains a constant 14°C. This is very unusual, as most lake waters this deep are usually a constant 4°C. Swarms of zooplankton can be seen around the sponges. These sponges are also similar in appearance to ones that have been observed in Froelicka Bay, Lake Baikal, Siberia (Crane et al. 1991; K.H. Nelson, personal observations); however, that comparison is only tentative as actual samples have yet to be recovered from this area, which is approximately 1 km deep.

Our video footage reveals an extremely complex, convoluted, and rugged bot-

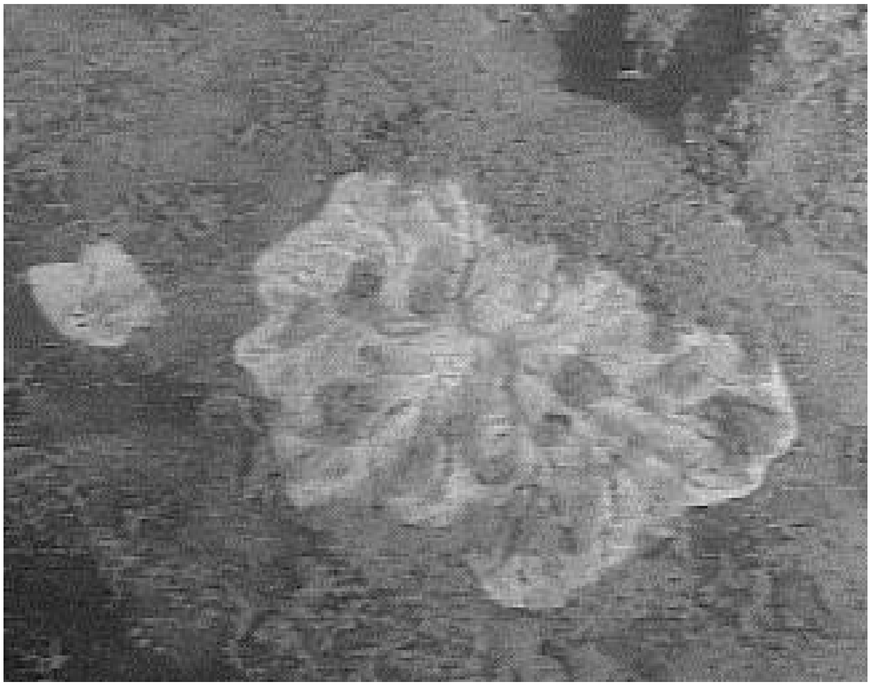

Figure 7. Close-up photograph, grabbed from video, of a "flat" sponge attached to a hard substrate (hydrothermal relict) at about 50 m in Mary Bay, Yellowstone Lake. Video by David Lovalvo, Eastern Oceanics, Inc.

tom topography unexpected in what, in a typical lake, would be the deep profundal basins of the system. For whatever reasons, seismic activity, venting, slumping, etc., these deep basins are not filled in with postglacial sediments, even though sedimentation in Yellowstone Lake is active and evident. Bottom sediments are deeply sculptured, most likely by periodic scouring by water forces that we have not yet observed (Klump et al. 1995).

Hot water vents are fairly common in these deeper parts of Mary Bay, and it is here that we discovered the freshwater equivalent of a "black smoker." On a routine dive in Mary Bay in 1995, after a relatively unsuccessful day, we came upon a vent that was obviously quite hot. The typical shimmering effect caused by hot vent water mixing with cold lake water was evident from quite some distance away, but what was most interesting was the fact that the hot-water plume had a dark color to it that clearly distinguished it from the water all around it. It was the closest we have come to a black smoker. When we measured the temperature, using an Onset recording thermistor, we found it to be approximately 115°C (Figure 8; Buchholz et al. 1995; Maki et al. 1995; Maki et al. 1996). Surrounding the vent were leeches. Some of them were feeding on the bacterial mat material that formed a halo around the vent and covered the vent opening like a flap; however, a number of them were dead, something we have since

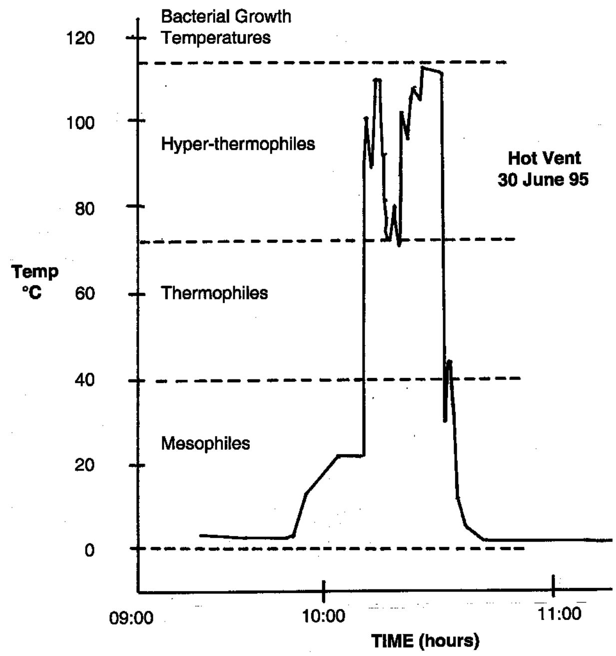

Figure 8. Temperature profile of a hot water vent in deep waters of Mary Bay (about 50 m), Yellowstone Lake. Manipulator arm of the ROV, with attached recording thermistor, was placed within the vent opening. Note that maximum temperatures of the vent water reached 115°C. The figure also indicates the temperature ranges for different classes of heat-tolerant to heat-loving microorganisms.

observed on numerous occasions. It would appear that these saprophytic leeches are attracted to these hot vents by the bacteria that grow nearby. These bacteria, usually sulfide-oxidizing, chemosynthetic bacteria, are utilizing the hydrogen sulfide in the hot water as an energy source and are thus able to grow and reproduce quite nicely. The leeches find them to be a tasty morsel and prey on them. Unfortunately for the leeches, however, many of these hot-water vents behave as geysers in that they have been seen to flow intermittently. Some leeches, eager to reach the bacteria on top of the vent, may periodically meet with very hot water suddenly erupting out of the vent. The result is boiled leeches. Through the eye of our ROV, these unfortunate victims, boiled white, stand out as beacons in its light.

In the deeper areas of the lake, off Stevenson Island for example, the features we observed most frequently were small depressions or openings in bottom sediments, 2.5–7.5 cm in diameter, from which an occasional gas bubble was emitted. Gas bubbles were not always seen, however, and we assumed that, based upon the loose, flocculent nature of these sediments, some relatively recent and persistent physical disturbance would be required to prevent the covering over and filling in of these depressions with sediment. Some of these small openings were also frequently surrounded, even covered, by a mat or film of stringy bacteria that fluttered and moved as warm or hot water flowed out of the vent, as well as white material that we assumed was elemental sulfur. In fact, after the first year or so, we used the white halo as a beacon indicating sulfide oxidation and the presence of bacteria.

Occasionally, warm or hot water was observed flowing from a fissure or openings in the bottom, creating a shimmering effect against a backdrop of cooler waters. The most dramatic example of this was observed at a depth of over 375 ft in a narrow depression in the main basin of the lake near Stevenson Island, where water in excess of 125°C was observed flowing from a small vent. This narrow, deep defile represented a sounding more than 14 m deeper than any before recorded in Yellowstone Lake. Sediments throughout this region were warmer than bottom waters by more that 5–7°C, and were even warmer still near presumed thermal features.

ROV observations of the bottom of the lake have revealed steep topography, sediment slumping, and "outcrops" of exposed sediment strata. If our estimates of deposition rates apply, these sediments are geologically quite young, no more than a few hundred to a couple of thousand of years old at most. They appear to be very well lithified, however, in contrast to sediments collected in other deep areas of the lake in cores nearly 3 ft in length. The sediments in Yellowstone Lake are a diatomaceous ooze consisting of up to 50-60% biogenic silica and having an organic carbon content of about 3%. It is possible that the exposed outcrops we see off Stevenson Island represent older sediments or that they have undergone accelerated lithification due to heating from below (Klump et al. 1995).

Among the more spectacular discoveries were the incredible cliffs in the deep canyons off Stevenson Island (Figure 9) in waters that reach 120 m or more. When we began to study the lake in detail, the recorded depth of Yellowstone

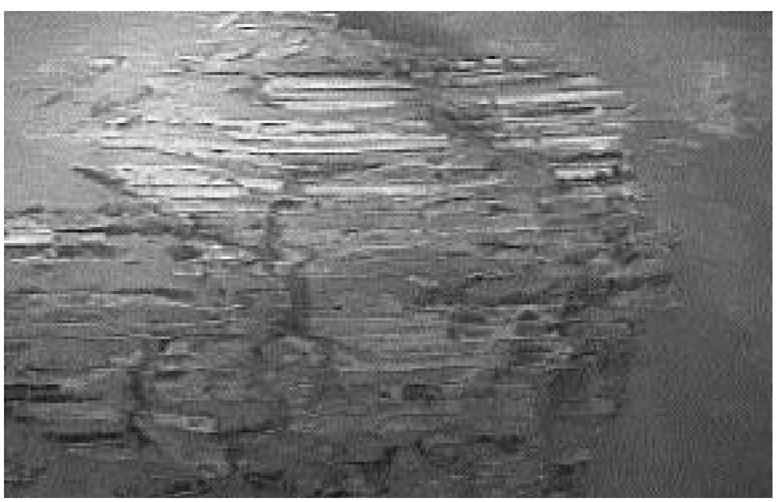

Figure 9. Photograph, grabbed from video, showing a panoramic view of spectacular cliffs in deep water (about 120 m) off Stevenson Island in Yellowstone Lake. Video by David Lovalvo, Eastern Oceanics, Inc.

Lake was 97.5 m. With our little robot submarine, however, we soon discovered that there were holes in the lake basin that went a great deal deeper. At the time we felt that there are areas of the lake that may well be deeper than 120 m, perhaps hiding more secrets that await discovery. In 1999, a side-scan sonar survey of the northern portion of Yellowstone Lake, conducted by the U.S. Geological Survey, Eastern Oceanics, Inc., and the University of Wisconsin–Milwaukee's WATER Institute, indicated depths off Stevenson Island reaching 137 m.

In 1987 and 1988 we conducted 12 dives off Stevenson Island in these deep and frigid waters. Incredible sights welcomed our eyes as we maneuvered our small robot down steep cliffs criss-crossed with cracks and fissures, and into narrow crevices and deep trenches. Cliffs of recently deposited and lithified sediment rose 50 to 75 ft and showed incredible structure. Rocky ledges that suddenly turned 90˚ with dramatic outcroppings were visible to us through the video eye of our small robot (Remsen et al. 1990). Occasionally, large, rounded hummocks of silty material appeared, on which were distributed, in a random fashion, stones or rocks of various sizes. These large, rounded hummock slopes often showed hot-water seeps or vents, identified by the presence of precipitated sulfur produced by the oxidation of sulfide by sulfide-oxidizing bacteria (Figure 10).

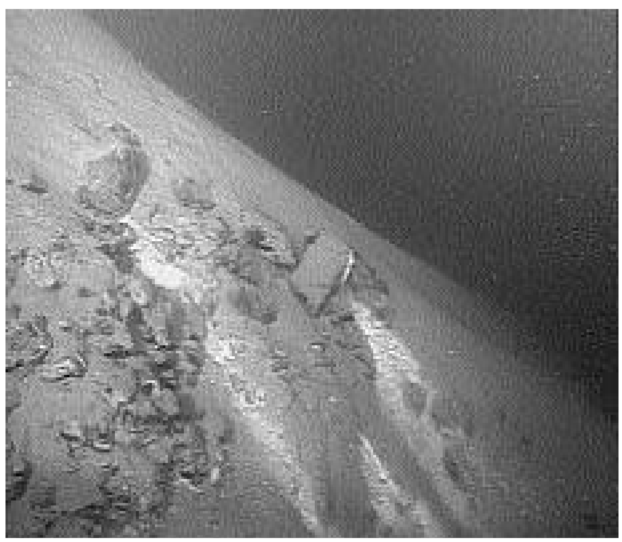

Figure 10. Photograph, grabbed from video, showing a panoramic view of a sediment slope, deep (about 100 m) in waters off Stevenson Island, Yellowstone Lake. Note the presence of hot water "seeps" or vents (arrow), identified by the presence of precipitated sulfur produced by the oxidation of sulfide by sulfide-oxidizing microorganisms. Video by David Lovalvo, Eastern Oceanics, Inc.

Hot water vents and fumaroles were almost always found at the base of these incredible cliffs in the waters off Stevenson Island (Figures 11 and 12). Sometimes they were hidden among the rocks and debris at the base of these

Figure 11. Photograph, grabbed from video, of a hot water vent in deep waters (about 135 m) off Stevenson Island, Yellowstone Lake. Again note the precipitated sulfur. Video by David Lovalvo, Eastern Oceanics, Inc.

Figure 12. Photograph, grabbed from video, of a hot water vent in deep waters off Stevenson Island, Yellowstone Lake. Note the accumulation of precipitated sulfur and sulfide-oxidizing microorganisms near the vent opening. Video by David Lovalvo, Eastern Oceanics, Inc.

underwater hills or mountains. These were often revealed by the white halo produced by sulfide-oxidizing bacteria living off of the hydrogen sulfide gas that was being emitted by the fumarole. Sometimes, however, they were simply identified by strange "caves" or "carvings" in the sediment cliffs. It became clear to us, after considerable thought and examining alternative explanations, that these features in the sediment were brought about by the action of hot water.

Finally, an intriguing discovery was made in 1992 while researching thermal areas in the West Thumb Basin, near the West Thumb thermal area. On advice from one of the local interpretive rangers, Jon Dahlheim, we began to search for—and found—what appeared to be an underwater geyser. With the ROV in position some 3 to 4.5 m down in a rocky, macrophyte-filled depression, a vent was discovered that periodically emitted large quantities of hot water. Initially erupting at approximately 20-minute intervals, a surprising observation was made: during each eruption, cutthroat trout appeared and actively swam into the roiling hot water, apparently feeding on particles of bacterial mat loosened by the action of the water. Further observations that year and in subsequent years confirmed our initial findings and the vent was dubbed the “Trout Jacuzzi.”

Evidence of Past Activity

Found on the bottom of the Mary Bay region, and serving as a surface for sponge colonization, were both small, hollow chimneys or pipe-like structures (Figure 13), about 12–25 cm in height and 4–7 cm in diameter, as well as larger irregular features. Preliminary X-ray diffraction studies and elemental analyses performed later in our laboratories at the University of Wisconsin–Milwaukee

Figure 13. Photograph, grabbed from video, of a hydrothermal relict pipe in bottom waters (about 50 m) of Mary Bay, Yellowstone Lake. Note attached sponge. Video by David Lovalvo, Eastern Oceanics, Inc.

indicated that these pipes consist of approximately 90% amorphous silica. Morphologically, and on a smaller scale, they resembled the carbonate (limestone) chimneys recovered from the outer continental shelf off northern Oregon (Kulm et al. 1988), and the so-called black smokers on the East Pacific Rise (Francheteau et al. 1979). We have hypothesized that these pipes are relict hydrothermal features that once served as conduits for hydrothermal fluids high in dissolved silica. Possibly formed below the sediment surface, the pipes may have become exposed following erosion of the surrounding (unconsolidated) sediment. Whether such hydrothermal plumbing exists under active vents has not yet been determined.

The pipes, or relict chimneys, that we discovered in the Mary Bay area seem to be more concentrated in the area we call the "Pipe Garden" (Remsen et al. 1990). For the most part, they are relatively small compared with the chimneys found in the marine environment.

The irregular features that have been seen range in size from rather small (5–8 cm in diameter) to quite large (up to 1 m in diameter). They usually are an amalgamation of connecting tubes molded together in a wide range of shapes. Others appear as if they were extruded from some strange mold and can be large mound-like structures, or thin, sheet-like structures sticking out of the side of a cliff or mound. In all cases, like the pipes, they consist almost entirely of amorphous silica. These concretions have not been observed outside of Mary Bay, certain areas off of Storm Point, and in the West Thumb area.

In 1996, thanks to some information provided by a NPS archeological survey team, transects were made over an area in Bridge Bay and the bottom was studied with a Furuno depth profiler (Figure 14). This work was rewarded with some spectacular sights: relict hydrothermal chimneys (Figure 15) that varied in height from 1.5 to 6 m and were covered with an incredible array of sponges, bryzoa,

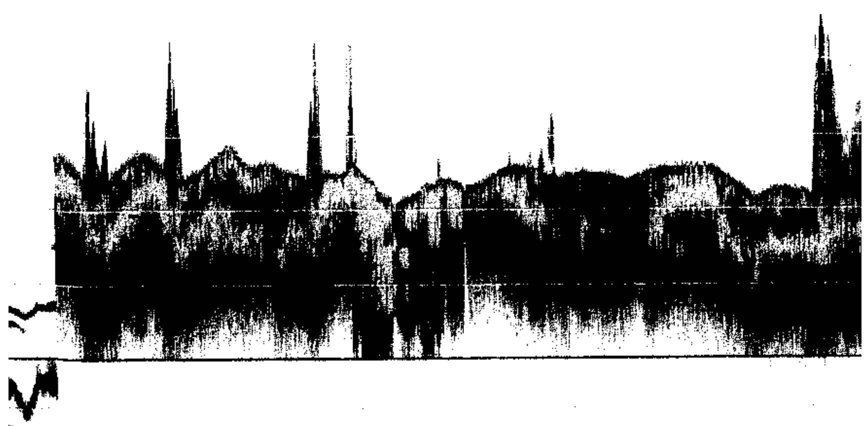

Figure 14. Sonar profile of an area of Bridge Bay, Yellowstone Lake. Note the spires (1 m to 10 m in height) rising from the bottom (about 20 m). These spires have been identified as relict hydrothermal chimneys.

and algae. These structures were analogous to the marine chimneys in their size and shape (Kulm et al. 1988), and, when active at some time in the past, must have been very similar to the hydrothermal chimneys that have been described in the marine environment.

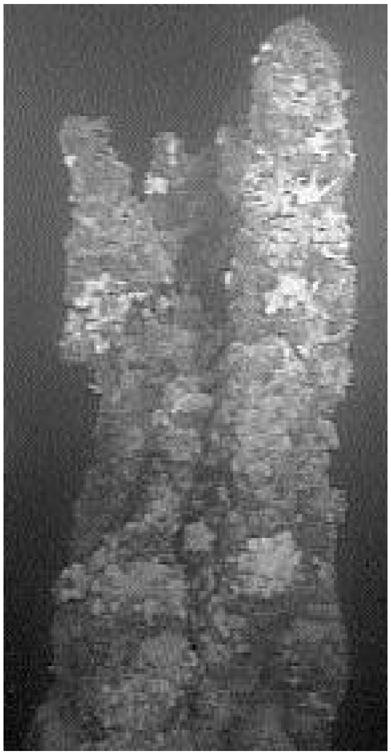

Figure 15. Photograph, grabbed from video, of a portion of a relict hydrothermal chimney in Bridge Bay, Yellowstone Lake. Note various sponges attached to the spire. Video by David Lovalvo, Eastern Oceanics, Inc.

General Conclusions

After a number of years of research on, and in, Yellowstone Lake involving SCUBA and ROV development, as well as sample collection and analysis, we are just now beginning to understand some of the dynamics at work, although the details are far from clear and will require continued research on our part. It is clear that the lake is richer than most high-altitude alpine lakes due to the nutrients that are introduced into it from the geothermal activity that we have just described. In addition, the microbial communities that exist in the lake as a result of this inorganic chemical input (chemosynthesis) contribute greatly to maintaining a thriving algal and zooplankton community. Furthermore, Yellowstone Lake may be subject to violent shifts in its underground plumbing caused by both minor and major earthquakes, and major sediment slumping events. These all have the potential to greatly influence the biology and chemistry of the lake.

In the deeper regions of the lake, off Stevenson Island for example, underwater hot springs and geysers are actively changing the landscape of the lake bottom by a variety of activities. On the one hand, constant streams of hot water carve out caverns in the sediment, exposing hard substrates through erosive power. In some areas, hot water simply oozes slowly out of a small vent, creating gradients of both nutrients and temperature that stimulate the growth of certain types of microorganisms. In other cases, chemicals in the hot water, such as methane or sulfur, can be used by these bacteria to produce new biomass or cell material—new biomass that is produced by chemosynthesis, not photosynthesis. As a result of these observations, we hypothesize that some of the sponges that we have observed in the deeper waters of Yellowstone Lake, as well as some of the plankton population that we find in swarms in deep waters, are sustained via a food chain driven by chemosynthesis. Thus in Yellowstone Lake, two life-driving forces—photosynthesis and chemosynthesis—are at work, as they are in the oceans where hydrothermal communities have been discovered.

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